

where young raptors raised on man-made substrates return as adults to nest on similar substrates, e.g., power line towers). My long association with Golden Eagles makes it difficult for me not to attribute short-term behavioral choices to experience, "intelligence," and communication between paired adults and between adults and their nestlings.

Whether the wind, sun, and visibility factors—or other undetectable habitat characteristics—are recalled by the eagles through conditioning, instinct, or "intelligence" is a fine point of debate. More important is the recognition that it does happen. It is part of their behavioral repertoire and should be incorporated into eagle habitat management plans—as well as development project designs, which involve lands where the absence or low quality of nest sites limit eagle population numbers. In this way complete territories can be created for raptors displaced by human activities, and we can add a tenth reason to our list of accomplishments which allow for a more positive outlook for eagles in the 1980s and 1990s.

WHAT IS THE FUNCTION OF UNDULATING FLIGHT DISPLAY IN GOLDEN EAGLES?

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Abstract

Undulating flight displays of the Golden Eagle (*Aquila chrysaetos*) have been interpreted as serving mostly pair bond maintenance or courtship functions. Fifteen displays performed by several individually recognizable pairs of Golden Eagles were witnessed in northern Colorado over a 6 year period. Most displays seemed to be stimulated by and directed at intruders known to be within the home range, suggesting an aggressive and territorial function of the display. Gender specific defense of the territory was also indicated. Copulation was observed during all seasons, but was never associated with undulating display. Evidence is presented suggesting displays of eagles in winter are an expression of seasonal territoriality rather than pair bond maintenance. The function of undulating flight display may be determined by observing the responses of eagles displayed to, or by distinguishing subtle differences between displays performed for courtship pair bond maintenance and those for aggressive territorial reasons.

Introduction

Undulating flight displays (Brown and Amadon 1968: 95; Fig. 1) of Golden Eagles have been witnessed and described many times (Bent 1937, Jollie 1943, Gordon 1955, Snow 1973, Brown 1977, Ellis 1979), and in nearly all instances the behavior was considered to be mainly sexual. Arnold (1954) stated that such aerial displays were included in

courtship activities of Golden Eagles, and Brown and Amadon (1968) considered undulating flight to be "purely nuptial or sexual in function". Bent (1937) regarded the display as often "merely joyful exercise" but primarily a "compulsion" to maintain the pair bond, and Brown (1977) felt that undulating display is one stage in a progression of specific epigamic or nuptial displays. Because the majority of Golden Eagle studies have concentrated on behavior only during the breeding season, the relationship of undulating flight displays to sexual function may have been overemphasized.

The context of undulating flight displays in some accounts suggest aggressive or territorial function to the behavior. Kochert (1972) watched an adult eagle undulate then chase an immature eagle from the territory; but no mention was made of a relationship between the display and aggression. Ellis (1979) noted that undulating flight was most often performed by territorial adults during the breeding season, hinting that the behavior may also function in territory defense. Brown (1977) stated that eagles are stimulated to undulate in the presence of intruders, also suggesting an alternative or additional function of the display, but he concluded that aerial undulations of eagles are "most likely to be in nuptial display than attacking or hunting". Brown (1977) also felt that displays of raptors in winter served primarily a pair bond maintenance function, but displays during the nonbreeding season may be more indicative of seasonal territoriality. Migrant Rough-legged Hawks (*Buteo lagopus*), Steppe Eagles (*Aquila rapax*) and Bonellis' Eagles (*Hieraaetus fasciatus*) have been known to display on their wintering grounds (Brown 1977), but few studies of these species have been conducted during the nonbreeding season and none with identifiable individuals. It is possible that had the habits and spacing of the displaying birds been known, an intruder may have been recognized in the vicinity. Little Eagles (*Hieraaetus morphnoides*) and Wedge-tailed Eagles (*Aquila audax*) also display outside of the breeding season and often in response to an in-

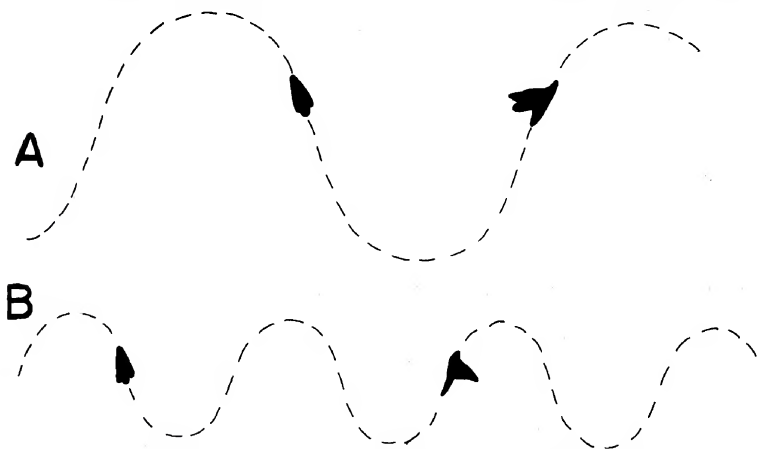


Figure 1. Relative amplitudes and frequencies of undulating flight displays of Golden Eagles at (A) high altitude (B) low altitude observed in northern Colorado, 1972-1979.

truder (S. Debus, pers. comm., Univ. of New England, NSW, Australia, 1981). I propose that the undulating flight behavior of Golden Eagles is primarily a territorial and threat display stimulated by the presence of intruders, while less frequently stimulated by reproductive drives for courtship or pair bond maintenance.

Methods

Observations were made in northern Colorado between November 1972 and March 1979 in connection with studies of resident adult and fledgling Golden Eagles, as part of biologistwarden duties on the National Audubon Society's Eagle Rock Sanctuary and during summer and winter raptor banding operations. During 6 years of field work, I became familiar with habits and ranges of many Golden Eagle pairs. Individuals were often identifiable by plumage characteristics, behavior with a mate, habitual movements through their range, use of "preferred" perches and association with nest sites. In addition, I witnessed displays of 2 of 4 resident radio-tagged adults. Conspecific intruders were often identifiable because of a lack of distinctive markers and general non-predictable use of the range, perches and roosts, and unfamiliar habits. Displays were often performed at extreme distances and quantification of certain components was therefore subjective; relative relationships, however, were obvious.

Results and Discussion

Fifteen undulating flights were observed (Table 1). The altitude, amplitude, and frequency of oscillations remained constant within each undulating display, but varied among displays. Low altitude displays (<100 m) seemed more intense, with undulations more frequent and with smaller amplitudes, than high altitude displays (Fig. 1). The intensity of a display seemed greater the closer an intruder was to a nest site or hunting area used by the resident pair. All displays terminated at approximately the same altitude they began. Seventy-three percent of observed displays occurred while an intruder was known to be within the home range of resident pairs and almost all were performed at low altitude. Ninety percent were performed while both mates were present. Displays in which just one member took part comprised 80%. In these instances, 66% were performed during winter months. In most cases, intruding eagles left the home range minutes after the initiation of the display, and the resident pair ceased undulations al-

Table 1. Circumstances of undulating displays by Golden Eagles observed in northern Colorado, 1972-1979.

Adult Pair	Displays Seen	Number			Mate Present	Intruder Seen	Species Displayed Against	Month of Occurrence (#)
		Male	Female	Both				
Finger Eyrice	4	2	1	1	4	4	Golden Eagle	March (2)
							Ferruginous Hawk	January (1)
							Man	May (1)
IBP	4	1	1	2	3	3	Golden Eagle	January (2)
							Ferruginous Hawk	April (1)
								December (1)
Owl Canyon	2	2			1	1	Golden Eagle	November (1)
Park Creek	1	1						October (1)
Great Wall	1		1			1	Ferruginous Hawk	February (1)
Pawnee Breaks	2	1	1		1	2	Golden Eagle	June (1)
								January (1)
Iron Clad Rock	1	1			1	1	Golden Eagle	March (1)
								June (1)

most immediately thereafter. This suggests that the presence of an intruder rather than sexual drive stimulates most undulating flight displays.

An undulation display, involving a juvenile Golden Eagle displaying towards an intruding adult eagle, was observed in April 1974. A banded eagle, produced by a resident pair the previous season, was observed undulating and diving at an adult standing on the ground while his parents perched on fence posts nearby. After 12 min of displays interspersed with aggressive stoops, the intruding eagle took off and unhurriedly flew away. The juvenile ceased displaying less than a minute later. The age and aggressive stoops of this juvenile suggest that the undulation display was not an attempt at courtship or pair bonding, but an attempt to drive an intruder out of a territory.

The most convincing evidence that intruders induce the undulation display involved an aggressive interaction between 2 resident adults and 2 intruding adults. On 23 December 1974 at about 1515, the radio-tagged IBP female eagle (Table 1) was circling approximately 20 m over a large, isolated saltbush (*Atriplex spp.*) and sage (*Artemisia spp.*) flat surrounded by short-grass prairie. Abundant shrubs on the flat provided excellent cover and food for many jackrabbit (*Lepus spp.*) and cottontail (*Sylvilagus spp.*). The flat was 2 km southwest of the IBP eagles' nest site, and was used for hunting by those eagles during winter months more often than any other area in the home range. Seconds after being joined by her mate, the circling eagles dove in tandem toward an adult eagle, judged by size to be a female, perched on the ground. The intruder leaped and presented talons to the attacking pair but no contact was made. After 2 more passes the resident birds perched on separate knolls bordering the flat. While the residents perched, a small adult eagle (presumably a male and the intruder's mate) appeared. Two more attacks by the resident pair followed, interspersed with perching. Preceding the third attack, both resident eagles performed an intense undulating display, consisting of a series of low, quickly executed undulations with peaks approximately 15 m off the ground. In an ensuing period of 38 min all 4 adults performed low altitude undulating displays (Fig. 1, B) at least once, the resident pair many times. The intruding male was knocked off the vane of a windmill by the resident male; the resident female landed next to the intruding female, and excreted in her direction; and all eagles dived at their perched opponents at least once. The encounter culminated in a mid-air collision of the resident female who, while attacking from the air, was met by the intruding female leaping from the ground. The eagles then grappled with each other on the ground for over 2 hr. As darkness set in, the fight continued, and terminated only when I approached within 2 m of the combatants. Evidently, this was a battle for control of a prime hunting territory, and both pairs displayed as each claimed title to the area. Since neither relented, an intense fight ensued and, had it not been for my intervention, could have resulted in death for at least one of the eagles.

Defense of the territory may be gender specific. In the above conflict, the resident IBP female directed the majority of her undulations and aggressive dives towards the intruding female while the resident male directed most of his displays and dives toward the intruding male after he appeared. In addition, resident males were observed to perform 66% of all displays in which only one member of the pair participated, most of which occurred between March and May. During this season the females are occupied with incubation/brooding activities and were often fed by males. It is, therefore, the male who is most responsible for territory defense and food acquisition and likely to drift into other occupied territories stimulating defensive displays of adjacent pairs. M.

Lockhart (pers. comm.) observed a resident male chase an intruding male from his territory after the resident female had been soaring casually with the intruder. Olendorff (1973) watched Golden Eagles exchange incubation duties after which the female gained altitude and began undulating. Possibly the male watched an intruding female enter the territory and relieved his mate so she could defend the territory. Ellis (1979) watched an adult female leave her eyrie and grapple with an immature eagle in mid-air, after which the immature "left the area rapidly". Prior to the contact, the adult male had been soaring near the immature. Ellis (pers. comm.) felt that the immature was also a female. Gender specific territorial defense would facilitate rapid replacement of lost mates.

On 3 occasions, resident adult Golden Eagles undulated and subsequently chased Ferruginous Hawks (*Buteo regalis*). These encounters lasted only seconds and undulations were considerably less intense than those directed at other eagles. Potential competition for food may have been the cause for aggressive behavior as the diet of Ferruginous Hawks is similar to that of resident Golden Eagles in northcentral Colorado (Olendorff 1973).

In May 1978 and March 1979 the Finger Eyrie male performed a series of undulations apparently directed towards a human intruder. In both instances, as I approached on foot to within 150 m of the incubating female, the male left his most commonly used perch 200 m to the east of the nest. He then undulated vigorously less than 20 m from the ground and about 100 m in front of me. I immediately withdrew and he returned to his perch.

I have visited the Finger Eyrie at least once a year since 1972 and have driven within 150 m of the resident pair many times, all with the least possible disturbance. Perhaps, since the Bald Eagle (*Haliaeetus leucocephalus*) is known to recognize individual humans and vehicles (Edwards 1969), Golden Eagles do also and the Finger Eyrie male has come to recognize me as no more than an unwanted intruder.

Eagles may maintain pair bonds by behavior patterns other than display. Radio-tagged adult Bald Eagles were observed to copulate on the wintering ground (Harmata in prep.) but were not seen to display to mates over a 3 month period of intensive winter tracking, during migration nor prior to nest building and egg laying. Aerial cartwheeling displays believed to function in courtship and pair bond maintenance (Retfalvi 1965; Hancock 1970; Brown 1977), involving both adult and immature Bald Eagles, occurred during winter months but were always observed during aggressive aerial chases resulting from conflicts over food or infringement on individual space. Almost half (46%) of all undulating flight displays of Golden Eagles discussed here occurred during winter but were never observed in association with copulation. Copulation was observed several times and during all seasons but was pre-empted and/or followed by one or more of these activities: mutual soaring, rolling and foot touching (Brown 1977), cliff racing (as described for the Prairie Falcon, *Falco mexicanus*, Olendorff 1973) and long periods of perching close together. Bald and Golden Eagles in winter therefore appear to maintain their pair bond sexually and by close association rather than display, and the same may be true for several other species of large raptors.

Undulating Flight Display: Sexual or Territorial in Function? Territorial signals in vertebrates may be closely related with mating behavior (Wallace 1979), and displays of many avian species involve both sexual and aggressive tendencies (Hinde 1970). Un-

undulating flight displays of Golden Eagles have been previously reported as primarily being associated with sexual function while evidence presented here also indicates a relationship to aggression and territoriality. Two strategies for resolving these conflicting tendencies have been identified in other birds and may help in defining the function of undulating display of Golden Eagles:

(1) Courtship in birds, especially Tetraonids, is often initiated by aggressive behavior, as males display to females in the same way they would to competing males (MacDonald 1968, Hjorth 1970). Subsequent behavior of the male depends on stimuli the female presents and his internal state (Hinde 1970). Undulating flight displays of Golden Eagles may therefore be initially stimulated by aggression but the response of the bird being displayed to may dictate the ultimate function, i.e. courtship and pair bond maintenance from responses of a mate or aggression and territorial defense from responses of an intruder. Viewed in this context, the same display could serve two functions.

(2) In some species, displays that function in both agonistic and sexual situations may actually be separated by subtle differences in components, depending on the specific context in which they occur. The sexual function of pivoting displays in Goldfinches (*Carduelis spp.*) is often distinguished by a call seldom heard during agonistic encounters involving the same display (Hinde 1970). Courtship "follow flights" of the Turkey Vulture (*Cathartes aura*) differ from aggressive pursuits of intruders in that trailing birds do not drop their feet during stoops when courting a mate (Davis 1979). A difference in characteristics between high and low altitude undulating displays of Golden Eagles was noted (Fig. 1). Intruders were not known to be within the home range during most high altitude, low intensity displays. These displays could serve primarily a courtship/pair bond maintenance function while more intense low altitude undulating flights function as mostly territorial/aggressive displays. However, it is possible that high altitude displays may be totally aggressive responses to actual or imminent violations of territory at the fringes, performed at altitudes most obvious to intruders at a distance. In any event, a display elicited in these contexts would serve a specific, singular function.

Newton (1979) felt that displays given long after pair formation in the breeding season, were most likely given in response to an intruder. In animals that pair for extended lengths of time, aggression between mates recedes as they become more acquainted (Manning 1967). Golden Eagles are a monogamous, long-lived species and it is therefore likely that aggression between mates of well established pairs is minimal. With a major component of courtship display absent, subsequent displays will most likely be in response to intruders and function in territorial defense.

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